

## Phalangeal Morphology of the Paromomyidae (?Primates, Plesiadapiformes): The Evidence for Gliding Behavior Reconsidered

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**KEY WORDS** finger morphology; vertical climbing; vertical clinging; dermoptera

**ABSTRACT** A comparative morphometric analysis of isolated proximal and intermediate phalanges attributed to the paromomyids *Ignacius graybullianus* and *Phenacolemur simonsi* was undertaken to test the hypothesis that these fossil phalanges exhibit evidence of a dermopteran-like interdigital patagium. Linear dimensions were collected for the fossil phalanges and a comparative sample of associated proximal and intermediate phalanges representing extant tree squirrels, tree shrews, dermopterans (colugos), gliding rodents and marsupials, and prosimian primates. Quantitative data indicate that the proximal and intermediate phalanges of paromomyids are most similar in their overall shape to those of the dermopteran *Cynocephalus*. The proximal phalanges of paromomyids and colugos possess well-developed flexor sheath ridges and broad, high shafts, whereas the intermediate phalanges of these taxa are most similar to one another in their trochlear morphology. Discriminant analysis indicates that all of the paromomyid intermediate phalanges resemble those from colugo toes more so than those from colugo fingers. Moreover, the relative length and midshaft proportions of both the proximal and intermediate phalanges of paromomyids closely resemble those of several squirrels that lack an interdigital patagium. The following conclusions are drawn from this study: 1) paromomyids share a number of derived phalangeal features with modern dermopterans that may be indicative of a phylogenetic relationship between them, 2) existing intermediate phalanges of paromomyids are inconsistent with the "mitten gliding" hypothesis because they do not possess the distinctive length and midshaft proportions characteristic of colugo manual intermediate phalanges, and 3) paromomyids share with colugos and the scaly-tailed squirrel *Anomalurus* several aspects of phalangeal morphology functionally related to frequent vertical clinging and climbing on large-diameter arboreal supports. *Am J Phys Anthropol* 109:397–413, 1999. © 1999 Wiley-Liss, Inc.

Paromomyidae is a family of early Tertiary mammals traditionally included within the primate suborder Plesiadapiformes (Fleagle, 1988; Van Valen, 1995). Previous workers (e.g., Szalay and Delson, 1979; Szalay et al., 1987) proposed that Plesiadapiformes is the sister group of Euprimates (but for alternative views, see Wible and Covert, 1987; Kay et al., 1992). Beard (1989, 1990) and Kay et al. (1990), however, recently

suggested that the plesiadapiform family Paromomyidae shares a number of derived postcranial and basicranial features with living dermopterans. Beard (1990, 1993b)

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suggested further that the derived postcranial traits shared by paromomyids and extant dermopterans are not only indicative of a close phylogenetic relationship between the two but also indicate that paromomyids were "mitten gliders" like living colugos.

Modern mammals that glide between arboreal supports possess a skin membrane, or patagium, that extends between the fore- and hindlimb and increases the lift and drag of the animal when it is airborne (Thorington and Heaney, 1981; Thorington, 1984). Colugos differ from other gliding mammals such as gliding rodents and marsupials in that they possess an interdigital patagium between their fingers and toes (Pocock, 1926). Colugo fingers exhibit especially long intermediate phalanges (Leche, 1886; Shufeldt, 1911; Pocock, 1926) and, as Beard (1993b, p. 65) noted, "only the highly derived phalangeal osteology of these animals bears such a direct functional relationship to their patagium and associated gliding habits." Beard (1990, 1993b) argued that the isolated intermediate phalanges he attributed to the paromomyid *Phenacolemur simonsi* resembled those from the hand of extant colugos in being slender, straight, and significantly longer than the proximal phalanges. Beard's (1989, 1990, 1993b) functional analysis of these fossil specimens led him to conclude that paromomyids possessed an interdigital patagium like that of modern dermopterans, and therefore paromomyids were dermopteran-like "mitten gliders."

The hypothesis that paromomyids were mitten gliders has been challenged by both Krause (1991) and Runestad and Ruff (1995). Krause (1991) concluded that the inference of mitten gliding in paromomyids is based upon the assumption that the isolated paromomyid phalanges were assigned correctly to the hand and foot. Krause (1991) found that this assumption had not been validated by sufficient evidence. Beard himself stated (1989, p. 178) that "there is no direct evidence that any of the proximal phalanges known for *Phenacolemur* represent the manus as opposed to the pes," and (p. 183) "there is no direct evidence that any of the intermediate phalanges known for *Phenacolemur* represent the manus as opposed to the pes." Runestad and Ruff (1995) later

provided preliminary data indicating that the isolated phalanges attributed to Paromomyidae also resembled those of certain non-mitten-gliding mammals such as *Microcebus* in their length and relative midshaft dimensions. Moreover, Runestad and Ruff (1995) demonstrated that all modern gliding mammals share distinctive long bone diaphyseal dimensions not observed in the long bones of paromomyids. Thus, the question of whether or not paromomyids were mitten gliders is one that remains actively debated and is still unresolved (Martin, 1993).

Recent studies (e.g., Meldrum and Yuerong, 1988; Begun, 1993; Begun et al., 1994; Hamrick et al., 1995; Jungers et al., 1997) demonstrated that integrated functional and morphometric analyses can be applied to reconstruct the positional behaviors of fossil taxa based on their phalangeal morphology. Furthermore, Hamrick et al. (1995) showed that quantitative methods can be used successfully to attribute isolated phalanges of fossil anthropoid primates to the hand and foot. Our study used a comparative functional and morphometric approach in order to resolve the question of whether or not paromomyid phalanges exhibit evidence of a dermopteran-like interdigital patagium. The implications of these data for understanding the locomotor and postural behaviors of paromomyids, as well as for understanding archontan phylogeny, are discussed.

## MATERIALS AND METHODS

### Sample

The fossil phalanges included here for study are from the collections of the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. The nine fossils included for analysis are complete proximal and intermediate phalanges from the USNM collections attributed by Beard (1989) to either *Phenacolemur simonsi* or *Ignacius graybullianus* (Table 1). Krause (1991) suggested that certain phalanges attributed by Beard (1989) to *P. simonsi* might actually represent *I. graybullianus*, and vice versa. Our results and conclusions would not differ if the species allocations were switched for any of the fossil specimens, as long as the fossils remained attributable to the Paromomyidae.

TABLE 1. Fossil paromomyid phalanges included for study

Taxon <sup>1</sup>	Specimen number	Specimen
<i>Phenacolemur simonsi</i>	USNM 442248	Proximal phalanx
<i>Phenacolemur simonsi</i>	USNM 442249	Proximal phalanx
<i>Phenacolemur simonsi</i>	USNM 442250	Intermediate phalanx
<i>Phenacolemur simonsi</i>	USNM 442251	Intermediate phalanx
<i>Phenacolemur simonsi</i>	USNM 442252	Intermediate phalanx
<i>Phenacolemur simonsi</i>	USNM 442254	Intermediate phalanx
<i>Ignacius gray-bullianus</i>	USNM 442256	Proximal phalanx
<i>Ignacius gray-bullianus</i>	USNM 442253	Intermediate phalanx
<i>Ignacius gray-bullianus</i>	USNM 442255	Intermediate phalanx

<sup>1</sup> Taxonomic attribution according to Beard (1989).

TABLE 2. Extant sample included for comparative analysis

Taxon	Individuals	Proximal phalanges <sup>1</sup>	Intermediate phalanges <sup>1</sup>
Order Marsupiala			
<i>Petaurus breviceps</i>	4	13/14	9/14
Order Rodentia			
<i>Anomalurus beecrofti</i>	2	3/4	3/3
<i>Glaucomys volans</i>	4	13/12	13/12
<i>Sciurus niger</i>	4	11/12	9/12
Order Scandentia			
<i>Tupaia tana</i>	4	8/8	8/8
Order Dermoptera			
<i>Cynocephalus</i> sp.	4	14/15	14/12
Order Primates			
<i>Galago senegalensis</i>	4	10/10	9/9
<i>Tarsius</i> sp.	4	16/15	14/12

<sup>1</sup> Manual phalanges/pedal phalanges.

We therefore follow Beard's (1989) species allocations of the fossil specimens for ease of communication. Beard (1989) also included several partial proximal and intermediate phalanges (c.f., *P. jepseni*) from the University of Michigan and the United States Geological Survey collections in his analysis; however, due to the incomplete nature of these specimens they were excluded from this study. Phalangeal morphology was also examined in a large comparative sample of extant gliding and nongliding mammals representing five orders of therian mammals. The sample includes gliding rodents, marsupials, and dermopterans as well as nongliding, arboreal primates, tree shrews, rodents, and marsupials (Table 2). In all, 342 phalanges were measured, of which 181 were proximal phalanges and 161 were intermediate phalanges (Table 2).

### Measurements

The following nine measurements were taken on the fossil specimens as well as on associated proximal and intermediate manual and pedal phalanges of the extant taxa included in the comparative sample (Fig. 1): 1) maximum phalangeal length (L), from the most proximal and distal points on each phalanx; 2) midshaft breadth (MSB), from the medial and lateral margins of the phalanx at approximately midshaft; 3) midshaft height (MSH), from the dorsal and

ventral borders of the phalanx at approximately midshaft; 4) proximal articular breadth (PAB), from the most medial and lateral margins of the proximal articular surface; 5) proximal articular height (PAH), from the most dorsal and ventral margins of the proximal articular surface; 6) dorsal trochlear breadth (DTB), from the most medial and lateral margins of the phalangeal trochlea on its dorsal surface; 7) palmar/plantar trochlear breadth (PTB), from the most medial and lateral margins of the phalangeal surface on its ventral surface; 8) trochlear length (TL), from the most proximal and distal points on the trochlear surface; and 9) trochlear height (TH), from the most ventral and dorsal points on the trochlea. These linear dimensions were chosen for analysis because they capture functionally significant aspects of phalangeal shape discussed by previous authors (e.g., Meldrum and Yuerong, 1988; Beard, 1993b; Begun, 1993; Hamrick et al., 1995). Linear measurements were taken from the extant specimens using digital calipers, whereas metric dimensions were taken from the fossil specimens using a stereo light microscope with a reticle attachment.

### Statistical analysis

Statistical analyses were performed on log-shape ratios derived from the raw data

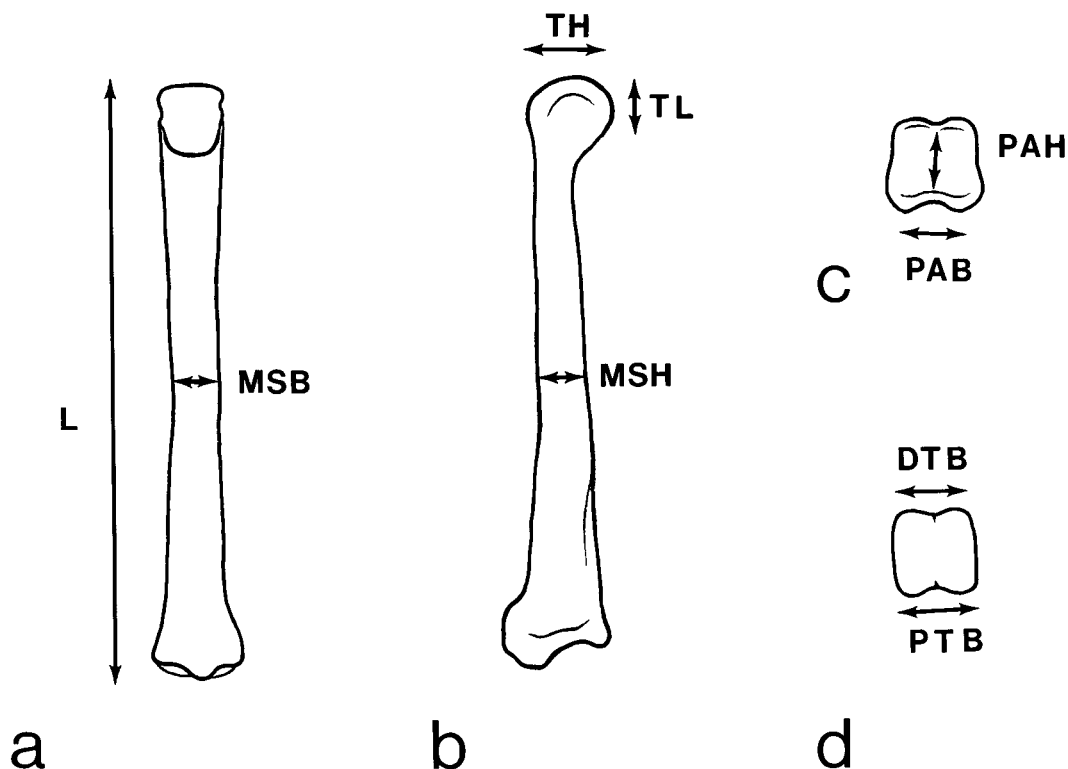


Fig. 1. Intermediate phalanx of a paromomyid in dorsal (a), lateral (b), proximal (c), and distal (d) views, showing linear measurements included for analysis. Measurement abbreviations are explained in text and in Table 3.

following the procedure described by Mosimann and James (1979), Falsetti et al. (1993), Jungers et al. (1995), and Hamrick (1998). Specifically, a size variable was created for each phalanx that was the geometric mean of all measurements taken on that phalanx. Each linear dimension on that phalanx was then divided by this size variable and logged to create a log-shape variable. The statistical analyses were chosen in order to answer two primary questions. First, what modern taxon possesses phalanges that are most similar in shape to those of the fossil taxa? Second, can the metric data be used to discriminate manual from pedal phalanges in the extant sample and, if so, then can we use these data to allocate the fossil phalanges to the hand and foot?

The first question was investigated using a multivariate principal components analysis (PCA) to summarize the osteometric data. PCA was the preferred multivariate technique

because the goal of the analysis was to explore variation in the metric data as well as examine the distribution of the extant and fossil specimens in multidimensional morphospace (Neff and Marcus, 1980; de Queiroz and Good, 1997). The proximal and intermediate phalanges were analyzed separately, but both the manual and pedal phalanges were included in each analysis. Visual inspection of the plotted PCA factor scores and examination of the log-shape ratio data allowed us to assess phenetic similarities in phalangeal morphology between the fossil and extant species. The second question, i.e., should each fossil phalanx be allocated to either the hand or the foot, was investigated using multivariate discriminant analysis. Two discriminant analyses, one including proximal phalanges and the other including intermediate phalanges, were run for the extant sample in order to test the hypothesis that phalanges from

TABLE 3. Mean and standard deviation (in parentheses) for proximal phalanx log-shape ratio values<sup>1</sup>

Taxon	L	MSB	MSH	PAB	PAH	DTB	PTB	TL	TH
Manual phalanges									
Pb	1.45 (.14)	-.39 (.11)	-.45 (.11)	.25 (.12)	-.08 (.59)	-.24 (.09)	-.07 (.07)	-.25 (.13)	-.20 (.12)
Ab	1.63 (.05)	-.35 (.12)	-.18 (.02)	.01 (.08)	.02 (.12)	-.42 (.10)	-.26 (.04)	-.08 (.02)	-.36 (.02)
Gv	1.64 (.06)	-.64 (.06)	-.55 (.10)	.12 (.08)	-.10 (.11)	-.13 (.08)	-.02 (.04)	-.01 (.04)	-.29 (.04)
Sn	1.51 (.05)	-.43 (.06)	-.50 (.08)	.24 (.07)	-.03 (.08)	-.31 (.14)	.01 (.04)	-.17 (.04)	-.31 (.05)
Tt	1.43 (.07)	-.44 (.08)	-.56 (.08)	.27 (.07)	-.05 (.11)	-.16 (.05)	-.05 (.03)	-.12 (.07)	-.30 (.04)
Cs	1.60 (.05)	-.32 (.08)	-.26 (.06)	.08 (.08)	-.08 (.06)	-.39 (.08)	-.27 (.03)	-.17 (.07)	-.17 (.09)
Gs	1.63 (.06)	-.41 (.05)	-.54 (.10)	.18 (.03)	-.02 (.04)	-.33 (.15)	-.05 (.06)	-.16 (.06)	-.27 (.06)
Ts	1.89 (.08)	-.48 (.08)	-.49 (.10)	.16 (.08)	.01 (.09)	-.39 (.17)	-.11 (.06)	-.28 (.08)	-.29 (.09)
Pedal phalanges									
Pb	1.36 (.13)	-.43 (.10)	-.39 (.11)	-.18 (.07)	.04 (.11)	-.21 (.08)	-.10 (.05)	-.18 (.09)	-.25 (.05)
Ab	1.49 (.12)	-.33 (.04)	-.14 (.13)	.03 (.04)	-.01 (.04)	-.31 (.04)	-.23 (.04)	-.19 (.08)	-.28 (.07)
Gv	1.64 (.65)	-.61 (.07)	-.61 (.05)	.21 (.04)	-.05 (.07)	-.11 (.04)	-.04 (.03)	-.07 (.11)	-.34 (.03)
Sn	1.57 (.04)	-.40 (.05)	-.46 (.09)	.28 (.07)	-.04 (.09)	-.30 (.15)	.02 (.03)	-.21 (.06)	-.44 (.08)
Tt	1.48 (.07)	-.43 (.08)	-.47 (.09)	.27 (.06)	-.06 (.07)	-.21 (.10)	-.06 (.02)	-.17 (.05)	-.33 (.08)
Cs	1.55 (.08)	-.25 (.05)	-.26 (.06)	.12 (.05)	-.14 (.11)	-.41 (.08)	-.28 (.14)	-.21 (.18)	-.10 (.16)
Gs	1.66 (.09)	-.50 (.10)	-.49 (.05)	.10 (.03)	.09 (.04)	-.30 (.05)	-.11 (.04)	-.15 (.05)	-.29 (.04)
Ts	1.86 (.10)	-.56 (.09)	-.51 (.07)	.21 (.05)	.07 (.09)	-.27 (.10)	-.06 (.06)	-.32 (.06)	-.40 (.09)
Fossil phalanges									
442248	1.69	.04	-.07	-.18	-.30	-.58	.01	-.22	-.39
442249	1.75	-.04	-.27	-.22	-.27	-.55	.01	-.11	-.27
442256	1.65	-.31	-.22	.04	-.24	-.34	-.06	-.12	-.37

<sup>1</sup> Pb, *Petaurus breviceps*; Ab, *Anomalurus beecrofti*; Gv, *Glaucomys volans*; Sn, *Sciurus niger*; Tt, *Tupaia tana*; Cv, *Cynocephalus sp.*; Gs, *Galago senegalensis*; Ts, *Tarsius sp.*; L, maximum phalangeal length; MSB, midshaft breadth; MSH, midshaft height; PAB, proximal articular breadth; PAH, proximal articular height; DTB, dorsal trochlear breadth; PTB, palmar/plantar trochlear breadth; TL, trochlear length; TH, trochlear height. Specimen numbers shown in the first column refer to fossil specimens described in Table 1.

the hand could be discriminated from those of the foot. Two discriminant analyses, one including proximal phalanges and the other including intermediate phalanges, were then run for phalanges of the mitten-glider *Cynocephalus* only. A separate pair of discriminant analyses was run for *Cynocephalus* because previous authors (Beard, 1990; Kay et al., 1990) suggested that paromomyids share a close phylogenetic relationship with modern dermopterans. Log-shape ratio values for the fossil paromomyid phalanges were entered into each analysis as unknowns and then classified as either hand or foot based on their factor scores. Posterior probabilities for group assignment are provided for each fossil specimen. USNM 442251 was excluded from the multivariate analysis because the damaged trochlea on this specimen prevented calculation of all measurements, and therefore precluded calculation of a log-size variable.

## RESULTS

### Proximal phalanges

Summary statistics for the proximal phalanx log-shape ratio values are shown in Table 3. Results of the principal components analysis performed on the log-shape ratio

values for the proximal phalanges included for study are shown in Figure 2a and Table 4. The first principal component axis accounts for approximately 33% of the variance and separates colugos, the scaly-tailed squirrel *Anomalurus*, and the paromomyids from the other taxa in the sample. Factor scores on this axis are most highly correlated with log-shape ratio values for midshaft dorsoventral height and mediolateral diameter (Table 4). The paromomyids, colugos, and *Anomalurus* each have low scores on this axis, and each exhibits relatively broad and high midshaft dimensions (Table 3). Similarities among these taxa in their proximal phalanx midshaft dimensions appear to reflect the very well-developed, proximally extensive flexor sheath ridges observed on the ventral surface of their proximal phalanges (Fig. 3). The second principal component axis accounts for approximately 18% of the variance and separates the primates and two of the fossil specimens, which have high scores on this axis, from the other taxa. This axis is most highly correlated (negatively) with proximodistal length of the trochlea, revealing that the paromomyids and primates tend to have trochleae that are quite short proximodistally. The third

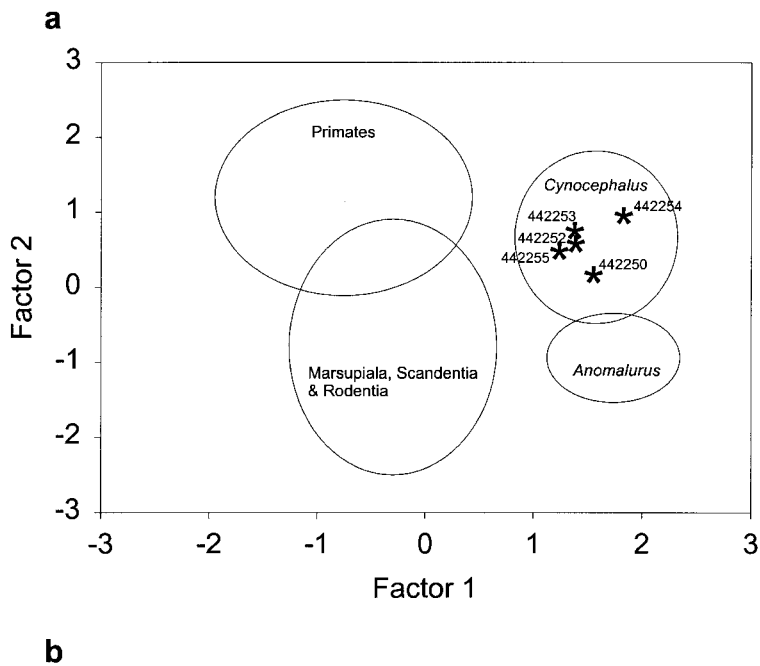
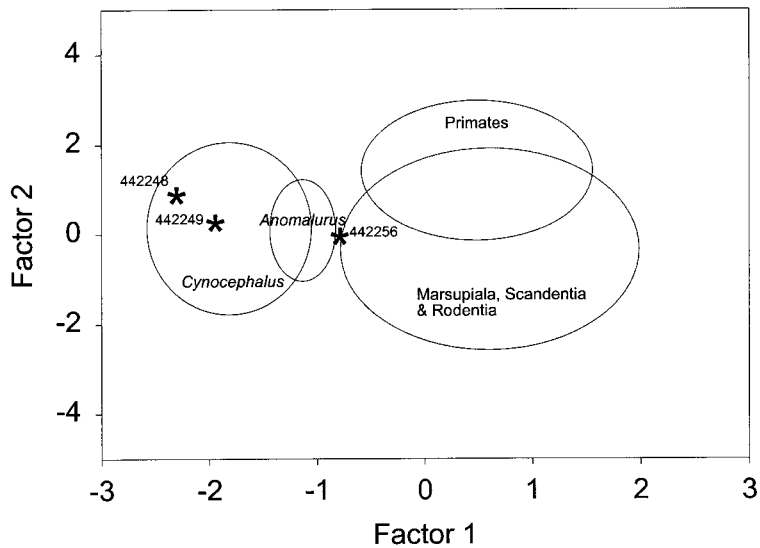


Fig. 2. Bivariate plots of factor scores for the first two principal component axes of (a) principal components analysis of proximal phalanx dimensions, and (b) principal components analysis of intermediate phalanx dimensions. Ellipses enclose the range of values for extant taxa. Fossil specimens are indicated by asterisks, and specimen numbers are shown on the plot.

principal component axis accounts for 14% of the variance and is mostly highly correlated (negatively) with breadth of the proximal articular surface. The primates, gliding squirrels, *Cynocephalus*, and the three fossil specimens have high scores on this axis, and all share proximal articular surfaces that are relatively narrow mediolaterally.

The discriminant analysis run on the proximal phalanx log-shape ratio data is successful in correctly classifying only 60% of the manual and 66% of the pedal phalanges in the entire comparative sample (Wilkes-Lambda  $F = 2.52$ ,  $P = 0.01$ ). The discriminant analysis classified all of the proximal phalanges of paromomyids to the



hand with posterior probabilities of 0.70–0.72. The discriminant scores are most highly correlated with height of the trochlea (Table 5). The manual phalanges have low discriminant scores and trochleae that are high dorsopalmarly, whereas the pedal phalanges have high scores and trochleae that are more compressed dorsoplantarily. When the discriminant analysis is performed on the log-shape ratio values for the proximal phalanges of *Cynocephalus* alone, the discrimination is highly significant (Wilkes-Lambda  $F = 5.24$ ,  $P = 0.001$ ) and correctly assigned

93% (27 of 29) of the colugo proximal phalanges to the hand and foot (Fig. 4a). The colugo discriminant analysis assigned the fossil specimens USNM 442256 and 442249 to the hand and USNM 442248 to the foot (Fig. 4a). Posterior probabilities are very high ( $P = 1.00$ ) for the assignment of specimens 442256 and 442248, but lower ( $P = 0.63$ ) for USNM 442249. The attribution of USNM 442256 and 442249 to the hand agrees with the assignment of Beard (1989). Beard (1989,

TABLE 4. Principal component loadings for the first three axes of the PCA performed on proximal phalanx log-shape ratio values

Measurement <sup>1</sup>	Factor 1 (33.2%)	Factor 2 (18.3%)	Factor 3 (14.0%)
MSH	-.88	.03	-.10
MSB	-.77	.01	-.41
PTB	.72	-.06	-.37
TH	-.59	-.42	.01
DTB	.59	-.55	.06
PAB	.51	.01	-.70
TL	.12	-.68	.49
L	.15	.60	.34
PAH	.26	.56	.30

<sup>1</sup> Measurement abbreviations are explained in Table 3.

TABLE 5. Pearson correlation coefficients (loadings) between discriminant scores and log-shape ratio variables included in discriminant analyses of manual and pedal proximal phalanges

Measurement <sup>1</sup>	Canonical loadings	
	Analysis with all taxa	Analysis with <i>Cynocephalus</i> only
L	-.19	.46
MSB	-.12	-.51
MSH	.19	.03
PAB	.40	-.38
PAH	.29	.33
DTB	.22	.14
PTB	-.12	.05
TL	-.34	.18
TH	-.46	-.33

<sup>1</sup> Measurement abbreviations are explained in Table 3.

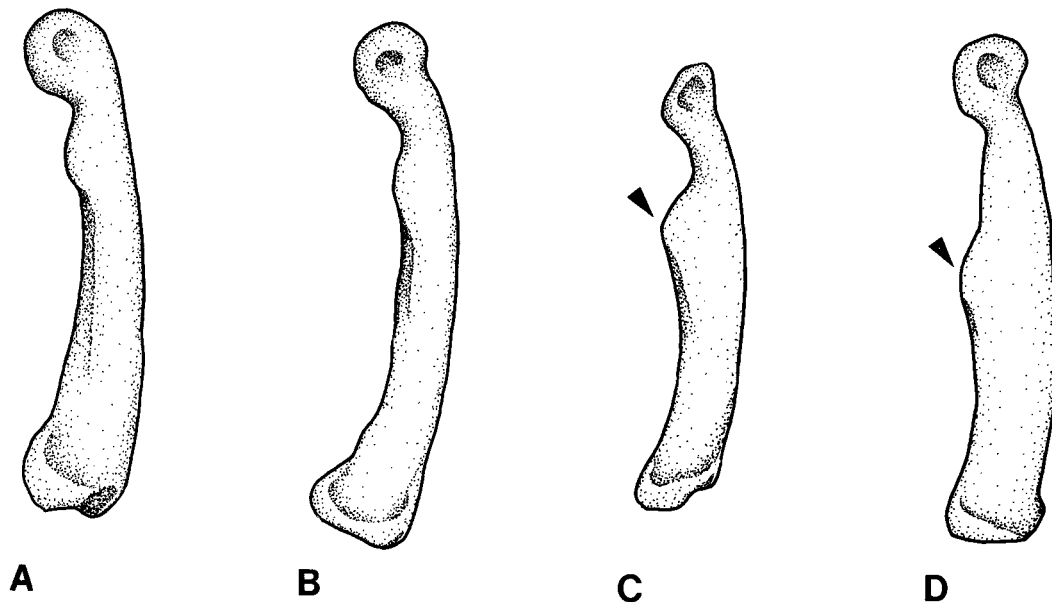


Fig. 3. Proximal phalanges of (A) *Tupaia*, (B) *Galago*, (C) *Ignacius graybullianus* (USNM 442256), and (D) *Cynocephalus* in lateral view. Arrows in C and D indicate the well-developed and proximally extended flexor sheath ridges of *Ignacius* and *Cynocephalus*. *Tupaia*, *Ignacius*, and *Cynocephalus* were modified and redrawn from Beard (1993b). Not to scale.

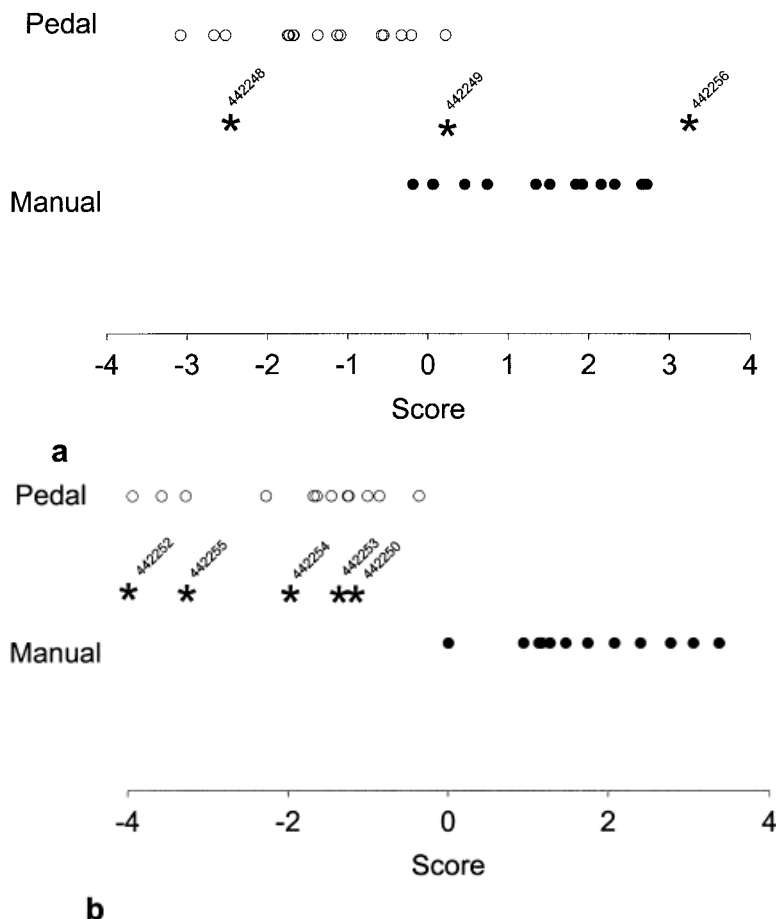


Fig. 4. Univariate plots of discriminant scores for discriminant analysis of (a) proximal phalanx dimensions and (b) intermediate phalanx dimensions in the dermopter *Cynocephalus*. Fossil specimens are indicated by asterisks, and specimen numbers are shown on the plot. Pedal phalanges are represented by open circles and manual phalanges are represented by solid circles.

1990) did, however, believe that USNM 442248 belonged to the hand of *P. simonsi*.

The discriminant scores for the analysis of colugo proximal phalanges are most highly correlated with log-shape ratio values for proximal phalanx length and midshaft diameter (Table 5). An index of proximal phalanx midshaft diameter relative to length, shown in Figure 5a, illustrates that colugo manual phalanges are slightly longer and more slender than their pedal phalanges. The relatively poor discrimination between manual and pedal proximal phalanges in the first set of discriminant analyses is due to the fact that the proximal phalanges of the foot are relatively more gracile than those from the hand in *Sciurus*, *Galago*, *Tarsius*, and *Tupaia*, whereas the reverse is true in *Cynocephalus*, *Glaucomys*, *Petaurus*, and *Anomalurus* (Fig. 5a). Thus, although relative mid-

shaft diameter can be used to separate manual from pedal phalanges within extant dermopterans, the same criterion cannot be applied across taxa. Moreover, it is clear from Figure 5a that the proximal phalanges of a mammal possessing an interdigital patagium do not differ significantly in their relative length and midshaft dimensions from those of a mammal that lacks an interdigital patagium.

#### Intermediate phalanges

Summary statistics for the intermediate phalanx log-shape ratio values are shown in Table 6. Results of the principal components analysis performed on the log-shape ratio values for the intermediate phalanges included for study are shown in Figure 2b and Table 7. The first principal component axis accounts for approximately 35% of the vari-



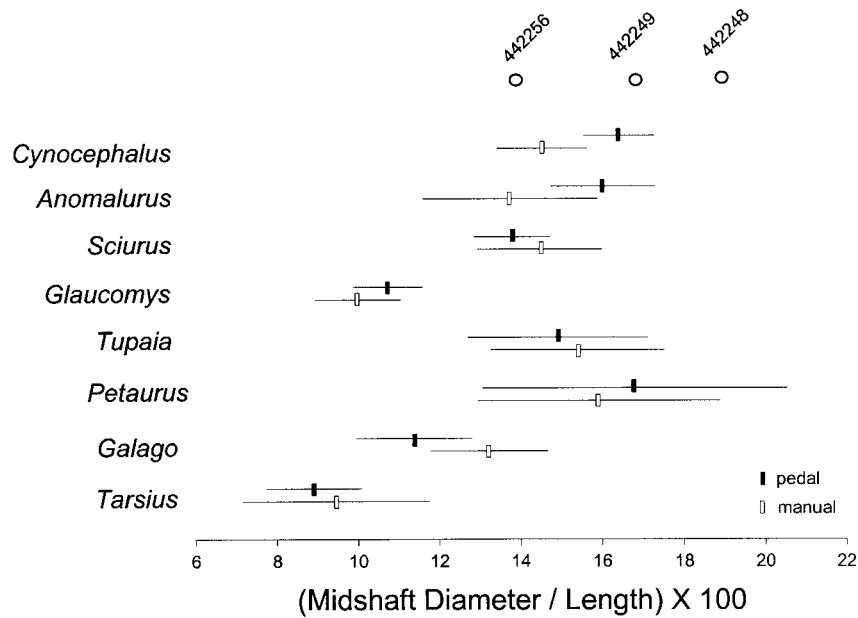
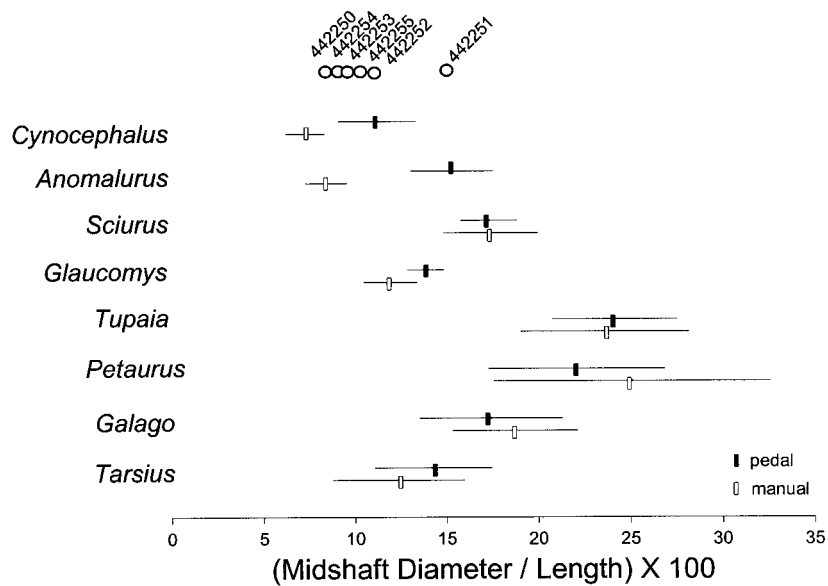
**a****b**

Fig. 5. Plots showing ratios of midshaft diameter to phalanx length for (a) proximal phalanges and (b) intermediate phalanges. Fossil specimens are indicated by open circles, and specimen numbers are shown on the plot. The vertical line in the middle of each box is the mean value, and the horizontal line represents one standard deviation. Manual phalanges are indicated by open vertical bars and pedal phalanges are indicated by solid vertical bars.

ance and separates *Cynocephalus*, *Anomalurus*, and the paromomyids, which has high scores on this axis, from the other taxa, which has low scores on this axis. This axis is most highly correlated with mediolateral breadth of the trochlea. Shape ratios indicate that *Cynocephalus*, *Anomalurus*, and

the fossil taxa have relatively low values for this dimension and therefore possess trochleae that are relatively compressed mediolaterally. The second principal component axis accounts for approximately 18% of the variance and separates the primates, *Cynocephalus*, and the paromomyids from most of the

TABLE 6. Mean and standard deviation (in parentheses) for intermediate phalanx log-shape ratio values<sup>1</sup>

Taxon	L	MSB	MSH	PAB	PAH	DTB	PTB	TL	TH
Manual phalanges									
Pb	1.06 (.23)	-.36 (.09)	-.38 (.06)	.21 (.05)	.01 (.05)	-.08 (.04)	-.06 (.06)	-.18 (.13)	-.18 (.09)
Ab	1.72 (.05)	-.75 (.08)	-.40 (.04)	.12 (.03)	.12 (.08)	-.46 (.05)	-.28 (.01)	-.08 (.03)	.03 (.02)
Gv	1.53 (.09)	-.61 (.03)	-.62 (.05)	.18 (.04)	-.04 (.15)	-.12 (.06)	-.13 (.06)	.01 (.09)	-.18 (.03)
Sn	1.35 (.13)	-.46 (.04)	-.53 (.03)	.21 (.07)	.02 (.09)	-.20 (.13)	-.09 (.04)	-.18 (.06)	-.11 (.03)
Tt	1.14 (.12)	-.31 (.10)	-.42 (.17)	.19 (.07)	-.05 (.09)	-.08 (.08)	-.01 (.05)	-.17 (.11)	-.28 (.11)
Cs	2.03 (.08)	-.63 (.11)	-.42 (.07)	-.05 (.08)	.09 (.06)	-.33 (.10)	-.23 (.05)	-.33 (.14)	-.10 (.06)
Gs	1.45 (.11)	-.26 (.08)	-.55 (.12)	.20 (.03)	.09 (.07)	-.09 (.18)	-.01 (.04)	-.32 (.08)	-.51 (.05)
Ts	1.73 (.20)	-.39 (.12)	-.51 (.07)	.22 (.05)	-.01 (.08)	-.15 (.13)	-.06 (.09)	-.33 (.17)	-.48 (.15)
Pedal phalanges									
Pb	1.05 (.13)	-.47 (.14)	-.45 (.07)	.14 (.05)	.05 (.07)	-.06 (.09)	-.06 (.08)	-.12 (.13)	-.07 (.09)
Ab	1.38 (.08)	-.50 (.09)	-.37 (.04)	.13 (.01)	.06 (.02)	-.34 (.10)	-.37 (.03)	.02 (.04)	.01 (.02)
Gv	1.42 (.02)	-.56 (.06)	-.59 (.06)	.21 (.03)	.02 (.04)	-.15 (.04)	-.15 (.03)	.01 (.07)	-.21 (.02)
Sn	1.34 (.05)	-.41 (.05)	-.43 (.05)	.28 (.06)	.01 (.07)	-.23 (.10)	-.11 (.04)	-.23 (.04)	-.21 (.16)
Tt	1.15 (.07)	-.27 (.07)	-.43 (.09)	.24 (.04)	-.07 (.05)	-.11 (.06)	-.04 (.03)	-.19 (.07)	-.27 (.04)
Cs	1.68 (.13)	-.51 (.08)	-.38 (.09)	.03 (.09)	.16 (.06)	-.34 (.07)	-.26 (.06)	-.27 (.09)	-.09 (.09)
Gs	1.43 (.14)	-.29 (.12)	-.54 (.08)	.20 (.03)	.06 (.10)	-.01 (.08)	.01 (.04)	-.34 (.06)	-.51 (.10)
Ts	1.52 (.23)	-.44 (.10)	-.48 (.10)	.16 (.13)	-.02 (.08)	-.06 (.14)	.05 (.09)	-.28 (.17)	-.43 (.14)
Fossil phalanges									
442250	1.82	-.62	-.33	.13	-.03	-.55	-.19	-.19	-.03
442252	1.75	-.48	-.32	.12	-.03	-.67	-.13	-.23	-.01
442253	1.82	-.50	-.27	.19	-.12	-.54	-.27	-.31	.01
442254	1.90	-.43	-.31	.04	-.01	-.68	-.23	-.23	-.04
442255	1.79	-.51	-.38	.02	-.03	-.56	-.06	-.22	-.03

<sup>1</sup> Abbreviations are explained in Table 3. Specimen numbers shown in the first column refer to fossil specimens described in Table 1.

TABLE 7. Principal component loadings for the first three axes of the PCA performed on intermediate phalanx log-shape ratio values

Measurement <sup>1</sup>	Factor 1 (35.62%)	Factor 2 (18.31%)	Factor 3 (14.23%)
PTB	-.84	.03	-.11
DTB	-.77	-.19	-.22
MSB	-.65	.43	.45
TH	.65	-.45	.36
PAB	-.64	-.09	.08
L	.57	.46	-.54
TL	.09	-.89	.03
MSH	.34	.36	.77
PAH	.40	.23	-.26

<sup>1</sup> Measurement abbreviations are explained in Table 3.

other mammals in the sample, including *Anomalurus* (Fig. 2b). Factor scores on this axis are most highly correlated with dorso-ventral height of the trochlea and phalanx length. Examination of the shape ratio data indicates that these taxa, which all have high scores on this axis, possess trochleae that are reduced dorsally and phalangeal shafts that are quite long (Fig. 6). The third principal component axis accounts for approximately 14% of the variance and is also highly correlated (negatively) with phalangeal length. The primates, gliding squirrels, and *Cynocephalus* have low scores on this axis and relatively elongate phalanges in contrast to the five fossil specimens, which

have high scores on this axis and comparatively lower values for relative phalanx length.

The discriminant analysis run on the intermediate phalanx log-shape ratio data for the entire sample is successful in correctly classifying only 64% of the manual and 62% of the pedal phalanges (Wilkes-Lambda F = 1.90,  $P = 0.06$ ). The discriminant analysis classified all of the intermediate phalanges of paromomyids to the hand with posterior probabilities of 0.68–0.75. The discriminant scores are most highly correlated with relative phalanx length (Table 8). The manual phalanges have high scores and long shafts when compared to the pedal phalanges, which have low scores and relatively shorter shafts. When the discriminant analysis is performed on the log-shape ratio values for the intermediate phalanges of *Cynocephalus* alone, the discrimination is highly significant (Wilkes-Lambda F = 7.28,  $P < 0.001$ ) and correctly assigned 100% (24 of 24) of the colugo proximal phalanges to the hand and foot (Fig. 4b). The discriminant scores are most highly correlated with log-shape ratio values for intermediate phalanx length and midshaft diameter (Table 5). An index of intermediate phalanx midshaft diameter relative to phalanx length shows that

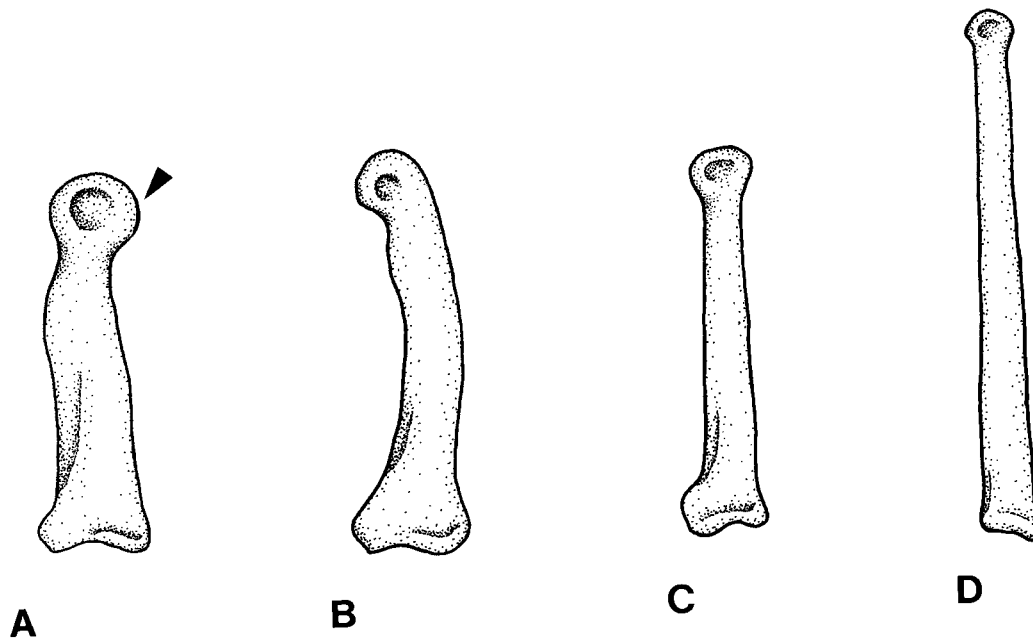


Fig. 6. Intermediate phalanges of (A) *Tupaia*, (B) *Galago*, (C) *Ignacius graybullianus* (USNM 442253), and (D) *Cynocephalus* in lateral view. Arrowhead in A indicates the dorsally expanded articular surface on the trochlea of *Tupaia*. *Tupaia*, *Ignacius*, and *Cynocephalus* were modified and redrawn from Beard (1993b). Not to scale.

TABLE 8. Pearson correlation coefficients (loadings) between discriminant scores and log-shape ratio variables included in discriminant analyses of manual and pedal intermediate phalanges

Measurement <sup>1</sup>	Canonical loadings	
	Analysis with all taxa	Analysis with <i>Cynocephalus</i> only
L	.84	.87
MSB	-.26	-.61
MSH	-.29	-.32
PAB	-.26	-.57
PAH	-.28	.02
DTB	-.31	.40
PTB	-.10	-.08
TL	-.21	-.32
TH	-.15	-.25

<sup>1</sup> Measurement abbreviations are explained in Table 3.

manual intermediate phalanges of *Cynocephalus* have low values for this index, whereas pedal intermediate phalanges have higher values (Fig. 5b). Thus, the manual intermediate phalanges of colugos are relatively longer and have narrower shafts than their pedal intermediate phalanges.

The discriminant analysis performed on colugo phalanges assigns all five of the fossil

specimens to the foot with very high posterior probabilities ( $P > 0.98$ ) for each assignment (Fig. 4b). Note that this classification is precisely the opposite of that obtained when the discriminant analysis is run for all taxa in the comparative sample. USNM 442251, excluded from the multivariate analysis because of its damaged trochlea, has a relatively high midshaft diameter/length ratio like the other intermediate phalanges. We therefore suggest that USNM 442251 be classified in the same manner as the other specimens in each analysis (Fig. 5b). The attributions of USNM 442250, 442251, 442252, and 442255 to the foot agree with the assignments of Beard (1989). Beard (1989, 1990) did, however, believe that USNM 442253 belonged to the hand of *I. graybullianus* and USNM 442254 belonged to the hand of *P. simonsi*.

The two discriminant analyses, one run for the entire sample and one run only for *Cynocephalus*, classified the paromomyid phalanges differently in each analysis. The plot of intermediate phalanx midshaft

breadth relative to length shown in Figure 5b provides some insight into why the two discriminant analyses differ in their attribution of the fossil specimens. Colugos possess manual intermediate phalanges that exhibit the lowest values for this index; however, colugo pedal intermediate phalanges also have quite narrow midshafts for their length. The discriminant analysis run on intermediate phalanges for the entire sample misclassified 10 of the 26 colugo intermediate phalanges. All of these misclassified colugo phalanges are pedal phalanges that were assigned to the hand by the discriminant function. Thus, the pedal intermediate phalanges of colugos are quite similar in their relative length and midshaft dimensions to the manual intermediate phalanges of non-"mitten-gliding" mammals such as *Tarsius* and *Glaucomys* (Fig. 5b). This explains why the paromomyid intermediate phalanges were classified differently in the two discriminant analyses: the intermediate phalanges of paromomyids are similar in their relative length and midshaft dimensions to those from the hand of vertical clingers (e.g., *Tarsius* and *Glaucomys*) as well as those from the foot of *Cynocephalus*.

## DISCUSSION

### Functional morphology of paromomyid phalanges

The manual and pedal proximal phalanges of paromomyids exhibit a number of features related to powerful flexion of the fingers and toes. Foremost among these features are the well-developed flexor sheath ridges. The flexor sheath ridges on the proximal phalanges of *Ignacius* and *Phenacolemur* are pronounced and flare both ventrally and laterally, creating a concavity between the ridges on the ventral phalangeal surface. Qualitative and quantitative data presented here indicate that the morphology of this region in paromomyids resembles that observed in proximal phalanges of the colugo *Cynocephalus* and the scaly-tailed gliding squirrel *Anomalurus*. *Anomalurus* frequently clings to vertical tree trunks, and the scales on the ventral surface of its tail stabilize the animal during clinging postures by interlocking with the trunk surface (Nowak, 1991). Bristles on the ventral surface of the tail in

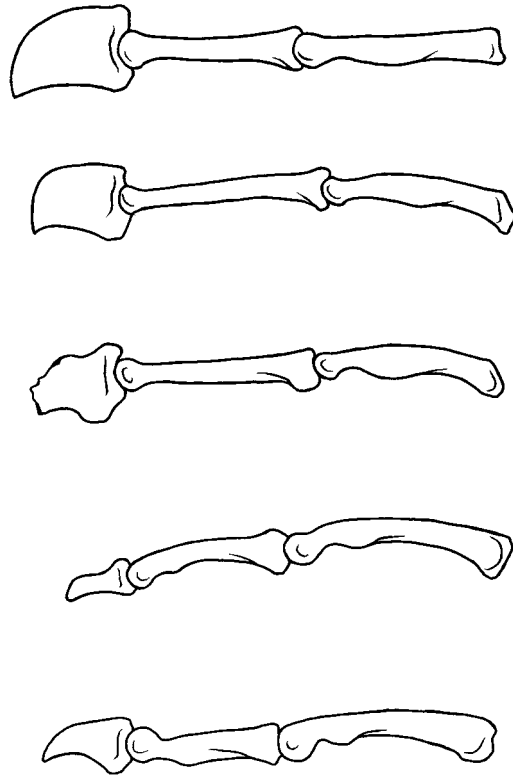


Fig. 7. Third digits in lateral view of (top to bottom) *Anomalurus beecrofti* (manual), *Cynocephalus volans* (pedal), *Phenacolemur simonsi* (USNM 442248 and 442250, and USGS 17847), *Galago crassicaudatus* (pedal), and *Tupaia glis* (pedal). Note similarities in morphology of the proximal, intermediate, and distal phalanges among *Anomalurus*, *Cynocephalus*, and *Phenacolemur*. Not to scale.

woodpeckers serve a similar function (Richardson, 1942). *Cynocephalus* is also known to frequently cling to large-diameter vertical supports, and both *Cynocephalus* and *Anomalurus* climb up vertical trunks after landing at the end of a glide (Wharton, 1950; Lekagul and McNeely, 1977; Nowak, 1991). Colugos and scaly-tailed flying squirrels (and possibly paromomyids; see Szalay and Lucas, 1993) also share terminal phalanges that are very deep proximally and distally and compressed mediolaterally (Fig. 7). This morphology again appears related to their habit of frequent clinging and climbing on vertical tree trunks, using interlocking between their well-developed claws and the arboreal substrate (Feduccia, 1993). Additional aspects of paromomyid proximal pha-

lanx morphology related to frequent and forceful flexion at the proximal interphalangeal joints have been discussed in detail by Beard (1993b), and include strong dorsoventral curvature of the shaft and ventral extension of the articular surface on the trochlea. These data together suggest that paromomyids were capable of frequent and forceful flexion of the proximal interphalangeal joints of the hand and foot, typical of animals that frequently use vertical postures and climbing in an arboreal environment.

The intermediate phalanges of paromomyids, like the proximal phalanges, also exhibit features related to the use of vertical arboreal supports. The first of these features is the ventrally extended and dorsally restricted articular surface on the trochlea. The ventrally extended trochlear articular surface provides a large area of articular contact between the intermediate and distal phalanges when the distal interphalangeal joint is flexed. In contrast, arboreal mammals such as tree shrews, which often extend their terminal phalanges at the distal interphalangeal joints (Jenkins, 1974), possess dorsally expanded articular surfaces on their trochleae (Fig. 6). The intermediate phalanges of colugos and *Anomalurus* also resemble those of paromomyids in having trochleae that are compressed mediolaterally. Mediolateral compression of the trochlea on the intermediate phalanx is correlated with the mediolateral compression of the distal phalanx in these taxa.

The robusticity indices for the intermediate phalanges (Fig. 5b) also illustrate that paromomyids share with tarsiers, gliding squirrels, and colugos intermediate phalanges that have quite narrow midshafts relative to their length. These comparative data suggest further that taxa that frequently use vertical arboreal supports in their locomotor and postural behaviors share relatively elongate and gracile intermediate phalanges, particularly on their fingers (Fig. 7). A similar pattern is observed in the pedal phalanges of tree-trunk-climbing birds (Richardson, 1942; Bock and Miller, 1959; Hildebrand, 1995; Clark et al., 1998). Bock and Miller (1959) suggested that the more elongate intermediate and subungual phalanges

of trunk-climbing birds enabled them to spread their toes far apart when clinging to vertical trunks. In the case of mammals, however, there is no reason why increasing the length of the intermediate phalanges would increase the span between the toes any more than would increasing the length of the proximal phalanges. An alternative explanation is that the long intermediate phalanges of vertical clingers increase the length of the distal portion of the digits, so that the hand and foot can effectively subtend a greater central angle on large-diameter, vertical, cylindrical, arboreal supports (Cartmill, 1985). Evidence from the phalanges of paromomyids therefore accords well with evidence from other regions of the paromomyid postcranial skeleton which suggests that vertical climbing and clinging were frequent locomotor and postural behaviors practiced by these animals (e.g., Beard, 1991).

Comparative functional analysis of paromomyid phalanges suggests that these mammals possessed capabilities for powerful digital flexion using well-developed claws. Extant clawed, arboreal mammals that possess similar capabilities for forceful finger and toe flexion utilize postural and locomotor behaviors such as vertical clinging and climbing in an arboreal environment. Evidence from the cheiridium as well as from the long bones suggests that paromomyids probably practiced each of these behaviors to at least some degree. Quantitative data presented here reveal that the intermediate phalanges of paromomyids do not possess the distinctive length and midshaft proportions that characterize those from the fingers of "mitten gliders." Existing phalanges of paromomyids, as well as previously described paromomyid long bones (Runestad and Ruff, 1995), therefore provide no conclusive evidence that paromomyids possessed a colugo-like patagium.

#### Significance of phalangeal morphology for understanding archontan phylogeny

Primate superordinal relationships have been widely debated in recent years (e.g., Pettigrew, 1986; Szalay et al., 1987; Wible and Covert, 1987; Adkins and Honeycutt, 1991; Bailey et al., 1992; Kay et al., 1992;

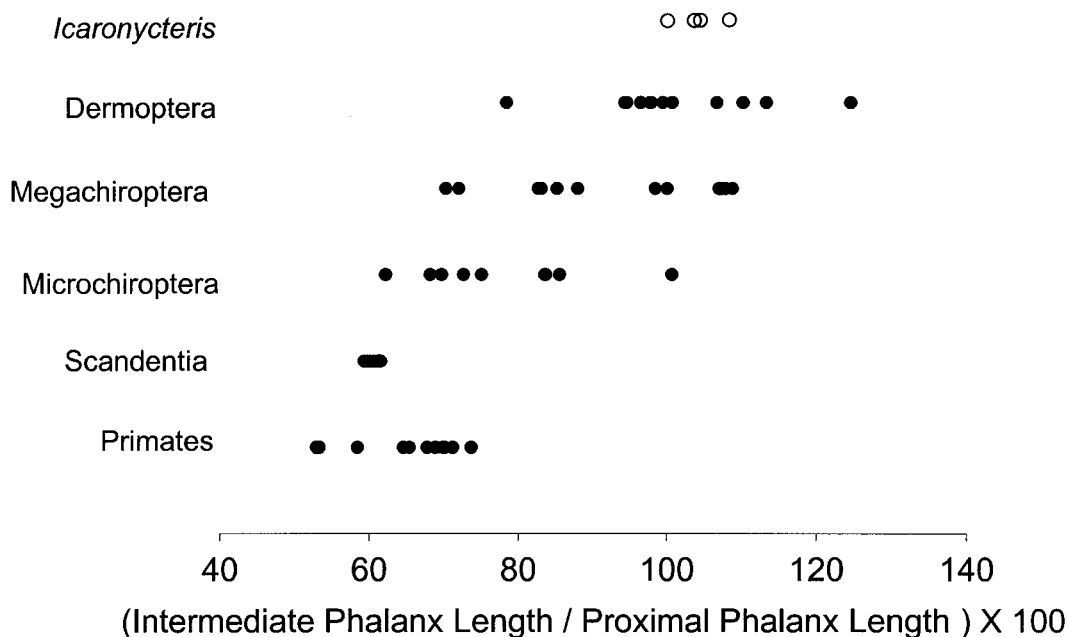


Fig. 8. Plot showing ratios of intermediate phalanx length to proximal phalanx length for toes II-V in various archontans. Primates include *Cheirogaleus medius* (n = 1), *Saimiri sciureus* (n = 1), *Loris tardigradus* (n = 1), *Galago senegalensis* (n = 2), and *Tarsius* sp. (n = 2). Scandentians include *Tupaia tana* (n = 4) and *Ptilocercus lowii* (n = 1). Microchiropterans include *Myotis lucifugus* (n = 2), *Eptesicus fuscus* (n = 2), and *Pteronotus parnelli* (n = 2). Megachiropterans include

*Pteropus hypomelanus* (n = 3) and *Rousettus amplexicaudatus* (n = 4), and dermopterans include *Cynocephalus volans* and *C. variegatus* (n = 3). Note that the bats and colugos both possess intermediate phalanges that are long relative to the length of their proximal phalanges when compared to the tree shrews and primates. Values for the fossil bat *Icaronycteris index* are from Jepsen (1966).

Novacek, 1992; MacPhee, 1993, and references therein). Postcranial evidence has figured prominently in these debates, usually in support of a phylogenetic relationship between primates and plesiadapiforms (e.g., Szalay et al., 1987; Beard, 1993a). Szalay and Lucas (1993) identified two derived characters from the cheiridium that support a phylogenetic relationship between dermopterans and bats: 1) ungual phalanges that are compressed mediolaterally and deep both proximally and distally (see also Yalden, 1985; Feduccia, 1993); and 2) elongation of the fourth and fifth pedal rays.

Our data suggest that bats and dermopterans share two additional derived character states of the cheiridium. First, chiropterans, including the fossil bat *Icaronycteris*, and dermopterans exhibit the derived conditions of having pedal intermediate phalanges that are elongate relative to their pedal proximal phalanges (Fig. 8; the same condition in

*Anomalurus* is interpreted as a convergence). The primitive eutherian condition, exhibited by tree shrews, squirrels, carnivores, insectivores, and primates, is to have pedal intermediate phalanges that are significantly shorter in length than the proximal phalanges. Thewissen and Babcock (1992) showed that bats and colugos are also derived in having intermediate phalanges on their fingers that are long relative to their proximal phalanges. Second, the intermediate phalanges of *Cynocephalus*, *Pteropus*, and paromomyids are distinctive in having proximal articular surfaces that are high dorsoventrally and compressed mediolaterally (Fig. 9). The primitive condition for Archonta is represented by tree shrews and primates in which the intermediate phalanx proximal articular surface is broad mediolaterally but more compressed dorsoplantarly. Colugos and bats also share a ratchet-like tendon-locking mechanism between the ten-



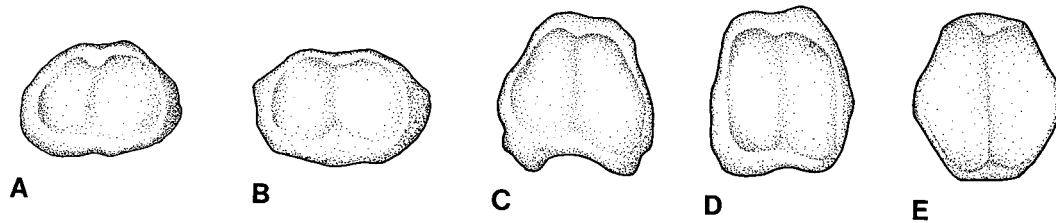


Fig. 9. Pedal intermediate phalanges of (A) *Tupaia*, (B) *Galago*, (C) *Ignacius graybullianus* (USNM 442253), (D) *Cynocephalus volans*, and (E) *Pteropus hypomelanus* in proximal view. Note the mediolaterally compressed and dorsoplantarly expanded proximal articular surfaces of the colugo, bat, and paromomyid. *Tupaia*, *Ignacius*, and *Cynocephalus* were modified and redrawn from Beard (1993b). Not to scale.

don of *m. flexor digitorum longus* and the fibrous flexor sheath that is derived for eutherian mammals (Bennett, 1993; Quinn, 1993; Simmons and Quinn, 1994). The majority of postcranial characters used previously to support a chiropteran-dermopterian clade were forelimb features related either directly or indirectly to the shared presence of a patagium (e.g., Wible and Novacek, 1988; Thewissen and Babcock, 1991; Stafford and Thorington, 1998). Our study indicates that bats, dermopterans, and paromomyids resemble one another in derived, phylogenetically significant aspects of phalangeal morphology that are not necessarily related to the presence of a patagial membrane.

### CONCLUSIONS

Comparative morphometric analysis of proximal and intermediate phalanges attributed to the paromomyid plesiadapiforms *Ignacius graybullianus* and *Phenacolemur simonsi* reveals that these fossil phalanges are most similar in their overall shape to those of the dermopterian *Cynocephalus*. The proximal phalanges of paromomyids resemble those of *Cynocephalus*, as well as those of the scaly-tailed gliding squirrel *Anomalurus*, in having well-developed flexor sheath ridges, whereas the fossil intermediate phalanges resemble those of *Cynocephalus* and *Anomalurus* in having distal articular surfaces that are expanded ventrally, reduced dorsally, and compressed mediolaterally. Discriminant analysis and robusticity indices suggest that the intermediate phalanges of paromomyids are most similar in their relative shape to those from the toes

of *Cynocephalus* and to those from the fingers of arboreal mammals that cling to vertical supports, such as *Tarsius*, *Glaucomys*, and *Anomalurus*. The hypothesis that paromomyids were "mitten gliders" is therefore not supported, since none of the existing paromomyid intermediate phalanges possess the distinctive length and midshaft proportions characteristic of colugo manual intermediate phalanges. Comparative functional analysis suggests that paromomyids were capable of forceful finger and toe flexion using clawed digits related to arboreal positional behaviors such as vertical trunk-clinging and -climbing. Finally, comparative analysis also demonstrates that bats, dermopterans, and possibly paromomyids share proportions and toe pedal intermediate phalanx articular surface morphologies that are derived among archontan mammals.

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